Influence of shade on soil and foliage water in a depleted short tussock grassland, Mackenzie Basin

Tony Payne & David A. Norton[1]

Rural Ecology Research Group, School of Forestry, University of Canterbury, Private Bag 4800, Christchurch 8140 New Zealand
[1]Corresponding author's email: david.norton@canterbury.ac.nz

(Received 27 July 2010, revised and accepted 6 October 2010)

Abstract

We assess the magnitude of shading on soil and foliage water content by manipulating environmental conditions to simulate the shade created by a woody cover in a degraded Mackenzie Basin short tussock grassland. We measured soil and foliage water content in 32 plots at two sites located in a stratified random split plot design over three months during the 2008/09 summer. Results showed that despite being a wetter and cooler summer than normal, both foliage and soil water contents were significantly higher in the shaded treatment compared to the unshaded treatment. We suggest that the shade associated with woody vegetation in degraded tussock grasslands is likely to create a moister environment for plants to inhabit, and that the loss of shade that occurred with historical deforestation in these ecosystems is likely to have decreased soil water levels. As a result, soil water content may well have decreased past the environmental tolerance of many native woody species limiting their ability to re-establish even if other factors such as seed availability and herbivory are not limiting, thus acting as a positive feedback for maintaining degraded tussock grasslands in their current state.

Key words: Artificial shade - degraded tussock grasslands - soil water - restoration thresholds - New Zealand.

Introduction

The extensive montane grasslands of New Zealand's eastern South Island high country represent a system that has been degraded as a result of unsustainable fire and grazing regimes, and more recently the invasion of exotic plants (O'Connor 1982; McGlone 2001; Espie 2001). These environments would have been dominated by woody vegetation prior to human settlement of New Zealand 7-800 years ago but are now dominated by degraded short-tussock grassland with the exotic forb *Hieracium pilosella* (Asteraceae) often the most abundant plant species, although scattered individuals of native tussocks (Poaceae; especially *Festuca novae-zelandiae* and *Poa colensoi*) and other native species still persist. Although now largely treeless, the vulnerability of

these grasslands to invasion by exotic woody species (Ledgard 2001; Sage *et al*. 2009) suggests that climatic conditions are still conducive to the growth of woody species. However, the ability of exotic woody species to establish and persist is not matched by native woody species that were present in these ecosystems historically. For example, experimental plantings of a range of native woody species have been very unsuccessful, with significant mortality and poor growth in remaining plants over a 4-year period notwithstanding the use of fertiliser, herbicide and grazing exclusion (Ledgard 2004).

As a result of the changes in vegetation composition due to anthropogenic disturbance, it seems evident that these high country ecosystems have crossed several ecological thresholds that are unlikely to be readily reversed (Hobbs & Norton 2004; Walker *et al*. 2009). Key thresholds associated with the inability of native woody species to re-establish in the high country include the loss of seed sources for many native woody species, intense competition from invasive species, especially *Hieracium pilosella*, grazing from domestic livestock and introduced lagomorphs (rabbits and hares), and the effect of changing vegetation composition on microclimatic conditions (e.g., soil water and winter frost). It is likely that all of these factors play a role in preventing the re-establishment of native woody vegetation.

In this study we focused on one of these ecological thresholds, changes in soil water conditions. In arid and semi-arid environments, shrubs and trees can act as "nurse plants" by increasing shade, allowing the establishment and persistence of other plant species (Geiger 1965). Shading results in alterations in the micro-climate beneath or adjacent to the nurse plant, including lower air and soil temperatures resulting in reduced transpiration and foliage water stress. Our objective was to quantify the magnitude of the shading effect on soil and foliage water content by manipulating environmental conditions to simulate the shade created by a woody cover.

Methods

Study area

Two sites, approximately 1 km apart, on ablation moraine dating from the end of the last glacial period (~ 13,000 years BP) in the Mackenzie Basin, eastern South Island, New Zealand (43° 54' S, 170° 26' E, 900 m elevation) were used. Both sites were level and located in the same farm management block thus subject to the same grazing regime. The area was lightly grazed by merino sheep (0.02 stock units ha^{-1} yr^{-1}; Norton *et al*. 2006) from October to December, but then ungrazed for the rest of the experimental period. Hares are however abundant through this area although their densities are unknown. The study sites are located in the rain-shadow of the Southern Alps. Mean annual rainfall at a site 10 km to the south is 592 mm (1925-2008), with the highest rainfall recorded over the winter months. Mean annual temperature is 8.8°C, with mean daily maximum and minimums of 21.4°C and 8.5°C in the warmest month (January) and 5.9°C and -2.8°C in the coldest month (July). Mean daily wind runs are high, averaging 315 km per day (2003-2009).

Soils have developed from loess and are upland Humose Orthic brown soils. The current vegetation is degraded hard tussock (*Festuca novae-zelandiae*) grassland with considerable bare ground and a dominance of *Hieracium pilosella* (Norton *et al*. 2006). A variety of other

native and adventive forbs and grasses are present, although woody species are rare. Woody species that do occur consist of sparse adventive wilding conifer species; native woody species, with the exception of cushion plants and subshrubs, are virtually absent. The pre-human woody vegetation cover is unknown, but most likely comprised a mixture of scattered trees (e.g., *Podocarpus cunninghamii*; Podocarpaceae), scrub (e.g., *Aristotelia fruticosa*, Elaeocarpaceae, *Coprosma* spp., Rubiaceae, *Corokia cotoneaster*, Agrophyllaceae, *Discaria toumatou*, Rhamnaceae, *Olearia odorata*, Asteraceae) and grassland (McGlone 2001).

Experimental Design

A stratified random split plot design was used to position 32 3.5 m ×3.5 m plots 3m apart at the two study sites; 20 plots were located at Site 1 and 12 at Site 2. The experiment ran from the 5 December 2008 to 8 March 2009 over the New Zealand summer. The 32 plots consisted of two factorial treatments; shading and grazing exclusion, resulting in four field treatments (shading + grazing, shading + no-grazing, no-shading + grazing, no-shading + no-grazing). The shading treatment comprised black shade-cloth with 65% light permeability 3.5 m² in area raised 1.5 m from the surface. The grazing exclusion treatment (excluding sheep and lagomorphs) consisted of a one metre high, wire mesh fence around the circumference of the plot with approximately 0.3 m of continuous fencing laid outwards from the perimeter of the fence and tightly secured to the ground with large rocks. The layout of the four treatments at both sites was random. There were five replicates of each treatment at Site 1 and three replicates at Site 2.

The floristic composition of each plot was recorded at the start of the experiment. Cover abundance of each vascular plant species was visually estimated within four 0.5 m x 0.5 m quadrats in each plot using a seven-point scale (1, ≤ 0.1%; 2, 0.1–0.9%; 3, 1–5%; 4, 5–25%; 5, 26–50%; 6, 51–75%; 7, 76–100%). Each quadrat was located at an equal distance from the plot centre to the perimeter along each diagonal. The data from the four quadrats was averaged for each plot prior to analysis.

Soil and foliage water content were then determined within each plot at the start of the experiment. Two soil samples (50-150 mm depth) were taken from each plot and combined in the field and immediately placed in a sealed plastic bag. *Hieracium pilosella* was chosen for determining foliage water content due to its high abundance and presence across all plots. Fifty *H. pilosella* leaves were randomly selected in each plot, with no more than two leaves coming from the same rosette. The leaves with their petioles attached were cut using scissors from the base of the plant and placed in a sealed plastic bag. Both soil and foliage samples were placed in a chilled container to reduce water loss immediately after sampling.

Soil and foliage samples were first collected on the 5 December 2008, with subsequent collections made on the 5 February 2009 and 8 March 2009. Samples were collected in the early morning to mitigate diurnal fluctuations in soil and foliage water content. Furthermore, sample collection was restricted to days that were preceded by at least two days of zero rainfall.

Laboratory Analysis

Soil and foliage samples were transported in the chilled container from the field site to the laboratory on the day they were

collected. Once in the laboratory the initial mass or fresh mass of each sample was recorded. Mass was recorded to 0.1 g using an electronic scale. Soil samples were then dried in an oven at 70°C for 72 h. Once dried, each soil sample's dry mass was recorded.

After the initial mass measurement each foliage sample was saturated with water by filling each sample bag with enough water to fully submerge all leaves for 24 h. Before each foliage samples saturated mass was recorded, the entire surface area of each saturated leaf was carefully dried off by blotting with paper towels. Each foliage sample was then dried in an oven at 70°C for 72 h. Once dried, the dry mass of each foliage sample was recorded.

Soil water content (W_{sc}) was measured using the fresh mass (f_s) and dry mass (d_s) of the soil samples:

$$W_{sc} = (f_s - d_s) / d_s$$

Relative foliage water content (W_{fr}) was measured using the fresh mass (f_f), saturated mass (s_f) and dry mass (d_f) of the foliage samples (Bannister 1986):

$$W_{fr} = (f_f - d_f) / (s_f - d_f)$$

W_{fr} is theoretically independent of the dry mass of the foliage material and is the complement of the water deficit (W_{fs}).

$$W_{fs} = 1 - W_{fr}$$

Statistical analysis

Daily climate data from the Lake Tekapo EWS station (available from cliflo.niwa.co.nz) was analysed from the period of December 2008 to February 2009. This included calculating the mean and standard error of the daily total rainfall (mm) and daily maximum air temperature (°C) for each month for December 2008 January 2009 and February 2009. The monthly climate data was also analysed from 1927 to the present. This included calculating the mean and standard error of the monthly total rainfall (mm) and monthly maximum air temperature (°C) for December, January and February.

Ordination of the floristic data was undertaken using Detrended Correspondence Analysis (DCA) as implemented in the computer program CANOCO (ter Braak & Smilauer 1998) to detect the underlying structure of the floristic data. DCA provides an indirect ordination of the species by plot data matrix identifying the dominant floristic compositional gradients independent of other factors. To facilitate interpretation of the dominant floristic gradients, species with single occurrences were removed prior to analysis. The percentage cover abundance data was square root arc-sine transformed and rare species were down-weighted for analysis. Single-factor analysis of variance (ANOVA) was then undertaken on the transformed data to compare ordination scores between shaded and non-shaded treatments for ordination axes 1 and 2 separately.

We analysed grazing, shade and time effects using split-plot ANOVA with either soil water or foliage water as the response variable. We used a nested error structure, with site treated as the highest scale (blocking) factor (unreplicated so no error term), with shading and grazing treatments within sites, and time was tested as a within-treatment effect. Plots were used as replicates for the grazing and shade effects, and time was treated as a within factor. Analyses were conducted in the base package of R v.2.8.1. (R Development Core Team 2009).

Results

The study sites experienced cooler and wetter conditions over the study period than is normal for this time of year (1927-2008 average; Figure 1). Rainfall in December was 198% average and in February 128% average, although January rainfall was below average (31%). Both December 2008 and February 2009 mean maximum temperatures (i.e., day time temperatures) were also below average (by 1.1 and 2.2°C respectively), while January mean maximum temperature was above average (by 1.3°C).

The pre-treatment vegetation comprised 34 vascular plant species, with the exotic forb *Hieracium pilosella* having the greatest cover and frequency (62% cover, 100% frequency) followed by the native grasses *Pyranthera exigua* (8% and 93%) and *Festuca novae-zelandiae* (2% and 78%). Bare ground also had a high cover (12%). The first two axes of the ordination explained 16.5 % and 11.8% of floristic variation, with gradient lengths of 1.37 and 1.43 SD units suggesting limited species turnover within the data set. The ordination diagram (Figure 2) shows that there is complete compositional overlap between shaded and non-shaded treatments at the start of the trial. There was also no significant difference (one-way ANOVA) in ordination scores between shaded and non-shaded plots for either Axis 1 ($F_{[1,30]} = 0.7$, $p = 0.40$) or

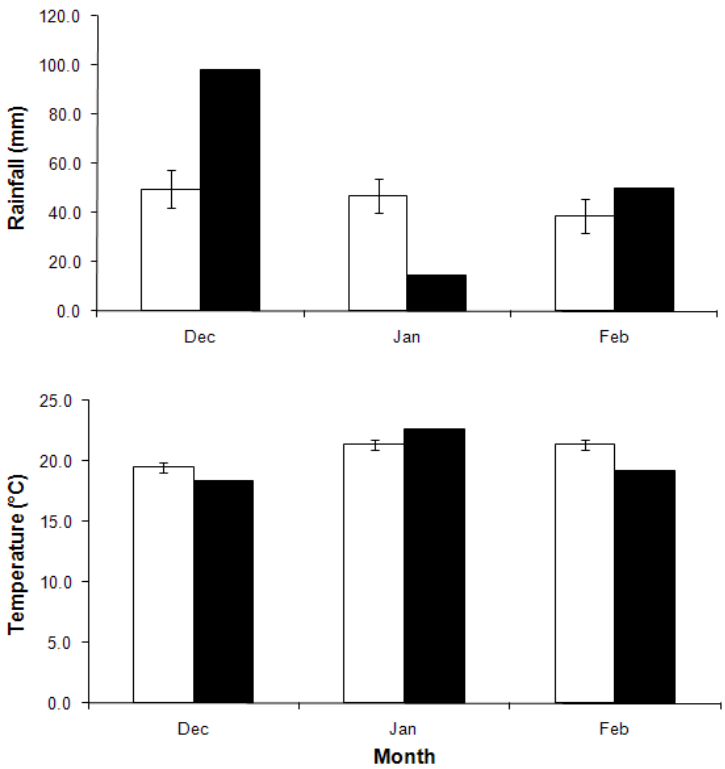

Figure 1. December – February 1927-2008 average (open bars ± 95% confidence intervals) and Dec 2008 – Feb 2009 (filled bars) Tekapo rainfall and temperature.

Axis 2 ($F_{[1,30]} = 0.4$, $p = 0.52$).

There was no significant effect of grazing on either soil and foliar water contents ($p = 0.37$; $p = 0.18$; Tables 1 & 2), nor was there any interaction between grazing and either shading or time for soil water ($p = 0.088$; $p = 0.90$; Table 1) or foliage water ($p = 0.71$; $p = 0.51$; Table 2). Grazing is therefore not discussed further.

There was no significant difference in water content of soil or foliage samples from shaded and non-shaded treatments at the outset of the experiment (Tables 1 & 2). However, over the three observations shade had a significant effect ($p < 0.0001$) on soil water, and this effect increased through time (shade x time interaction: $p < 0.0001$; Table 1; Figure 3). Although shade did not have a significant main effect on foliage water ($p = 0.1717$), there was a significant shade x time interaction ($p = 0.008$), as the shaded plants had increasingly more foliage water than the unshaded plants as the experiment progressed (Figure 3).

Table 1. ANOVA table for soil water content. Significant effects are in bold.

	df	SS	MS	F	*P*
Site:treatment					
Shade	1	0.0500	0.0500	14.7	**0.0007**
Grazing	1	0.0028	0.0028	0.8	0.3696
Shade x grazing	1	0.0107	0.0107	3.1	0.0879
Residual	27	0.0918	0.0034		
Total	30	0.1553			
Site:treatment:time					
Time	2	0.4964	0.2482	185.1	**<0.0001**
Shade x time	2	0.0655	0.0327	24.4	**<0.0001**
Grazing x time	2	0.0003	0.0001	0.1	0.8975
Shade x grazing x time	2	0.0004	0.0002	0.2	0.8517
Residuals	56	0.0751	0.0013		
Total	62	0.6377			

Table 2. ANOVA table for foliage water content. Significant effects are in bold.

	df	SS	MS	F	*P*
Site:treatment					
Shade	1	0.0048	0.0048	2.0	0.1717
Grazing	1	0.0047	0.0047	1.9	0.1772
Shade x grazing	1	0.0003	0.0003	0.1	0.7113
Residual	27	0.0659	0.0024		
Total	30	0.0757			
Site:treatment:time					
Time	2	0.5692	0.2846	138.0	**<0.0001**
Shade x time	2	0.0217	0.0109	5.3	**0.0081**
Grazing x time	2	0.0028	0.0014	0.7	0.5121
Shade x grazing x time	2	0.0027	0.0014	0.7	0.5205
Residuals	56	0.1155	0.0021		
Total	62	0.7119			

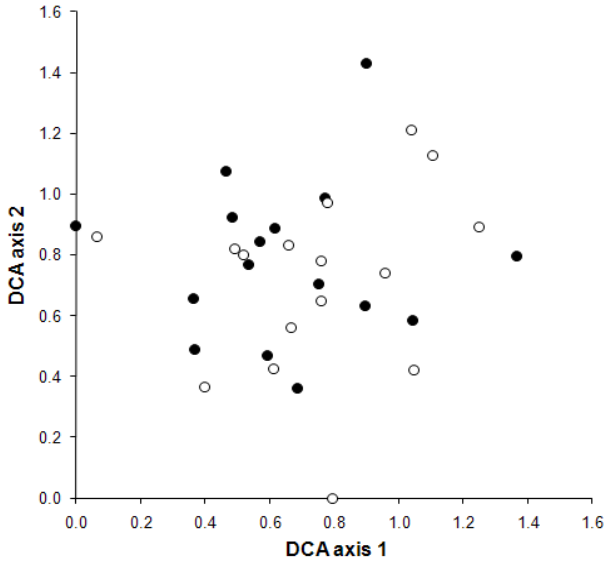

Figure 2. Ordination diagram showing floristic overlap of shaded (solid circles) and non-shaded (open circles) plots.

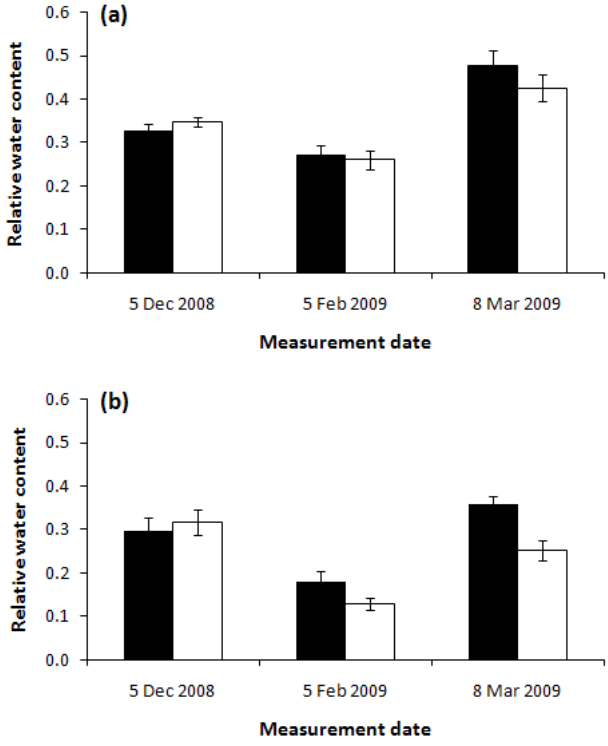

Figure 3. Changes in (a) foliage and (b) soil relative water content through time (overall means with 95% confidence intervals). Solid bars = shade treatment. Open bars = no-shade treatment).

Discussion

In this study we investigated one of the factors that is likely to play a role in limiting native woody species re-establishing in degraded high country grasslands, namely the role of shade in modifying soil water. Other likely limiting factors include loss of seed sources, intense competition from invasive species, grazing by both domestic livestock and introduced herbivores, and changes in other microclimatic conditions as a result of changing vegetation composition (e.g., winter frost).

Notwithstanding the unusually wet conditions over the summer study period, the shaded treatments had significantly higher soil water contents than non-shaded treatments. In environments similar to those we studied, foliage transpiration and soil evaporation usually represents the largest flux of water out of the ecosystem (Mitchell *et al*. 2009). It is well documented that shading reduces the amount of evaporation from the soil in a wide variety of ecosystems, and this effect is amplified in environments that experience marked summer soil water deficits. For example, in the sagebrush/bunchgrass steppe of the North American Great Basin, day-time soil water depletion significantly reduces under artificial shading due to a reduction in soil temperatures and evaporation (Williams *et al*. 1993). In semi-arid environments, artificial shading can reduce surface soil temperature extremes by up to 10-12°C, improving soil water status, in comparison with non-shaded plots (Wilson 1996). Furthermore, several studies in savanna ecosystems demonstrate that soil water in the top 150 mm of the soil is higher under the influence of shade from tree canopies due to a reduction of temperature and evaporation (Bernhard-Reversat 1982; Rhoades 1995).

A reduction in soil evaporation leads to an increase in the distribution of water in the vegetation rooting zone allowing an increase in the uptake of water by plants (Williams *et al*. 1993). Thus, parallel to increases in soil water, foliage relative water content also increased significantly under shaded treatments compared to non-shaded treatments. Other studies in semi-arid environments have shown an increase in foliage water content under shading (Rhoades 1995; Wilson 1996; Jefferson & Pennacchio 2005). Shading not only increases the available water in soils for plants, but also induces physiological responses that improve foliage water-use efficiency. Stomatal conductance and photosynthetic rate are highly correlated; consequently, when photosynthesis is reduced under shaded conditions, stomatal conductance increases, mitigating foliage water loss (Meziane & Shipley 2001). Thus, it appears that both an increase in available soil water and physiological responses causes a significant increase in the relative water content in plants under shaded conditions, and hence in plant survival (Padilla & Pugnaire 2009).

While closed canopy woody vegetation may result in increased transpiration compared to tussock grassland vegetation, at least in higher rainfall grasslands (Mark & Dickinson 2008), it seems likely that the pre-disturbance vegetation in the Mackenzie Basin would have been dominated by low forest, scrub and grassland (McGlone 2001) with correspondingly lower transpiration rates. Notwithstanding the potential of woody vegetation to reduce soil water levels through transpiration, the benefits of shade for plant survivorship and growth have been documented in similar environments to those studied here supporting the pro-

posed link between shade and soil water status. In particular, seedling survival and growth of both introduced legumes and wilding conifers has been shown to be significantly greater on the shady side of tall tussocks compared to other aspects (Scott & Archie 1976; Scott & Wallace 1978; Allen & Lee 1989).

The reduction in shade due to deforestation (Molloy *et al*. 1963; McGlone 2001; Rogers *et al*. 2007) is likely to have had an impact on soil water levels, amongst other factors, resulting in increased water stress for plants. Soil water content may well have decreased past the environmental tolerance of many native woody species limiting their ability to re-establish even if other factors such as seed availability and herbivory are not limiting, thus acting as a positive feedback for maintaining degraded tussock grasslands in their current state. This effect may well be exacerbated by the strong competitive effects *Hieracium pilosella* exerts on other plants for water as well as nutrients (e.g., Boswell & Espie 1998).

Acknowledgements

We thank Devon Christensen, Sam Gifford, Ali Karimian, Frisco Nobilly, Jonathon Pettigrew and Nigel Pink and field assistance, Will and Emily Murray for access to their property, Jason Tylianakis for assistance with statistical analyses, and Etienne Laliberté and David Whitehead for comments on earlier drafts of the manuscript. This research was supported by funding from the ARGOS project.

References

Allen, R.B. & Lee, W.G. (1989). Seedling establishment microsites of exotic conifers in *Chionochloa rigida* tussock grassland, Otago, New Zealand. *New Zealand Journal of Botany* 27: 491-498.

Bannister, P. (1986). Water relation and stress. In *Methods in Plant Ecology* (eds. P.D. Moore & S.B. Chapman), pp. 107-110. Blackwell Scientific Publications, London.

Bernhard-Reversat, F. (1982). Biogeochemical cycle of nitrogen in a semi-arid savanna. *Oikos* 38: 321-332.

Boswell, C.C. & Espie, P.R. (1998). Uptake of water and nutrients by *Hieracium pilosella* and effects on soil in a dry sub-humid grassland. *New Zealand Journal of Agricultural Research* 41: 251-261.

Espie, P. (2001). *Hieracium in New Zealand: Ecology and Management.* AgResearch, Mosgiel, New Zealand.

Geiger, R. (1965). *The Climate Near the Ground*. Harvard University Press, Cambridge, MA.

Hobbs, R.J. & Norton, D.A. (2004). Ecological filters, thresholds and gradients in resistance to ecosystem reassembly. In *Assembly Rules and Restoration Ecology* (eds V.M. Temperton, R.J. Hobbs, T. Nuttle & S. Halle), pp. 72-95. Island Press, Washington D.C.

Jefferson, L.V. & Pennacchio, M. (2005). The impact of shade on establishment of shrubs adapted to the high light irradiation of semi-arid environments. *Journal of Arid Environments* 63: 706-716.

Ledgard, N. (2001). The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management* 141: 43-57.

Ledgard, N. (2004). Establishing native seedlings in the high country. *High Country Forestry* 9: 2-3.

Mark, A.F. & Dickinson, K.J.M. (2008). Maximizing water yield with indigenous non-forest vegetation: a

New Zealand perspective. *Frontiers in Ecology and Environment* 6: 25-34.

McGlone, M.S. (2001). The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology* 25: 1-15.

Meziane, D. & Shipley, B. (2001). Direct and indirect relationships between specific leaf area, leaf nitrogen and leaf gas exchange. Effects of irradiance and nutrient supply. *Annals of Botany* 88: 915-927.

Mitchell, P.J., Veneklaas, E., Lambers, H. & Burgess, S.O. (2009). Partitioning of evapotranspiration in a semi-arid eucalypt woodland in south-western Australia. *Agricultural and Forest Meteorology* 149: 25-37.

Molloy, B.P.J., Burrows, C.J., Cox, J.E., Johnston, J. & Wardle, P. (1963). Distribution of subfossil forest remains in eastern South Island, New Zealand. *New Zealand Journal of Botany* 1: 68-77.

Norton, D.A., Espie, P.R., Murray, W. & Murray, J. (2006). Influence of pastoral management on plant biodiversity in a depleted short tussock grassland, Mackenzie Basin. *New Zealand Journal of Ecology* 30: 335-344.

O'Connor, K.F. (1982). The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *New Zealand Journal of Ecology* 5: 97-107.

Padilla, F.M. & Pugnaire, F.I. (2009). Species identity and water availability determine establishment success under the canopy of *Retama sphaerocarpa* shrubs in a dry environment. *Restoration Ecology* 17: 900-907.

R Development Core Team. (2009). *R: a Language and environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.

Rhoades, C. (1995). Seasonal pattern of nitrogen mineralization and soil water beneath *Faidherbia albida* (syn *Acacia albida*) in central Malawi. *Agroforestry Systems* 29: 133-145.

Rogers, G.M., Walker, S., Basher, L.M. & Lee, W.G. (2007). Frequency and impact of Holocene fire in eastern South Island. *New Zealand Journal of Ecology* 31: 129-142.

Sage, D.J.M., Norton, D.A. & Espie, P.R. (2009). Effect of grazing exclusion on the woody weed *Rosa rubiginosa* in high country short tussock grasslands. *New Zealand Journal of Agricultural Research* 52: 123-128.

Scott, D. & Archie, W.J. (1976). Seasonal variation in establishment of oversown seed in relation to tussock proximity. *New Zealand Journal of Experimental Agricultural* 4: 311-315.

Scott, D. & Wallace, A.R. (1978). Effect of ground cover and tussock proximity on legume establishment. *New Zealand Journal of Agricultural Research* 21: 93-105.

ter Braak, C.J.F. & Smilauer, P. (1998). *CANOCO Reference Manual and User's Guide to CANOCO for Windows: Software for Canonical Community Ordination* (Version 4). Microcomputer Power, Ithaca, N.Y.

Walker, S., Cieraad, E., Monks, A., Burrows, L., Wood, J., Price, R., Rogers, G. & Lee, B. (2009). Long-Term Dynamics and Rehabilitation of Woody Ecosystems in Dryland South Island, New Zealand. In *New Models for Ecosystem Dynamics and Restoration* (eds R.J. Hobbs & K.N. Suding), pp. 99-112. Island Press, Washington, D.C.

Williams, K., Caldwell, M.M. & Richards, J.H. (1993). The influence of shade and clouds on soil water

potential: the buffered behavior of hydraulic lift. *Plant and Soil* 157: 83-95.

Wilson, J.R. (1996). Shade-stimulated growth and nitrogen uptake by pasture grasses in a subtropical environment. *Australian Journal of Agricultural Research* 47: 1075-1093.